Quaternary Science Advances 14 (2024) 100185

Contents lists available at ScienceDirect

Quaternary Science Advances

journal homepage: www.sciencedirect.com/journal/quaternary-science-advances

Greening a lost world: Paleoartistic investigations of the early Pleistocene vegetation landscape in the first Europeans' homeland

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ARTICLE INFO

Keywords:
Paleoart
Paleoecology
Paleontology
Paleobotany
Pleistocene
Human evolution
Orce

ABSTRACT

The scarcity of pictorial reconstructions focusing on Quaternary flora and vegetation prompts a reevaluation of traditional zoocentrism in future paleoartistic research. Here we present paleoartistic renderings depicting vegetation landscapes around the Orce Archaeological Zone (OAZ), encompassing sites dating from 1.6 to 1.2 million years ago during the Early Pleistocene of the Guadix-Baza Basin in southern Spain. Four pieces are based on fossil pollen data from Venta Micena 1 (VM1), Barranco León (BL), and Fuente Nueva 3 (FN3). The artwork considers altitudinal belt distribution, taxonomic and structural diversity, extinct taxa in the Iberian Peninsula post-Early Pleistocene, and those previously extinct at higher latitudes in Europe. This essay visually represents the coexistence of mesophytic, thermophytic, and xerophytic plant communities within a glacial refugium of woody species. Lastly, employing a non-conventional iconographic approach, we portray a female *Homo* individual in the forest refugium to draw up on possible adaptive traits of these early Europeans.

> Contemplamus idem sidera. Caelum nobis commune est. Unum idemque coelum nos ambit. Quid refert quisque via mentis inquirat veritatem? Per unum iter non potest ad tam magnum arcanum perveniri (We contemplate the same stars. The sky is common to us. One and the same firmament envelops us. What does it matter through what mental process each one may seek the truth? By one path alone, so great a secret cannot be reached).
> Quintus Aurelius Symmachus (c. 340-402)

1. Introduction

1.1. Paleoart as an experimental subject and method for consilience

The process of paleoart typically begins with transferring scientific concepts to artistic expression. This involves sharing paleontological study materials and results in a series of experimental artistic outcomes (Amorós, 2023). The art critic and historian Nicolas Bourriaud (2015) asserts the possibility of considering artistic practice as a form of programming, allowing one to engage with shared reality and generate alternative versions of understanding: "through art, the non-definitive nature of the world is exposed, dislocated, reassembled, and imbued with disorder and poetry". From a less metaphysical perspective, Pulitzer Prize-winning evolutionary biologist Edward O. Wilson (2018) popularised that science and arts share the same brain processes of creativity (e.g. Andreasen and Ramchandran, 2012; McLeish, 2019). Scientists, however, are less accustomed to collaborating with creative artists and humanities scholars, perhaps because most of us pursue our careers and seek qualification and recognition in highly specialised investigative territories. As a result, the expression "the two cultures" was coined Snow (1961): the one represented by literary intellectuals -extensible to other fields of artistic creativity- and the other by scientific intellectuals. Between the two there would be a "gulf of mutual

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https://doi.org/10.1016/j.qsa.2024.100185
Received 10 February 2024; Received in revised form 14 March 2024; Accepted 21 March 2024

incomprehension" (Snow, 1961, p. 4). Although Snow's proposal has been widely criticised since its publication, in practice, many intellectuals have striven to maintain this distance. However, others have opted for dialogue and the search for common spaces of creation. In fact, Uzzi and colleagues have proposed that "the highest-impact science is primarily grounded in exceptionally conventional combinations of prior work yet simultaneously features an intrusion of unusual combinations" (Uzzi et al., 2013, p. 468). In this context, paleoart could well be an example of a third culture (Brockman, 1995) to bridge gaps in the search for consilience and the generation of excellent novel knowledge.

1.2. Paleoart: a gateway for bringing science to society

Invariably, paleoart will often have methodological gaps deemed insufficient to adopt an irrevocable dogmatic conclusion. However, it is advantageous that during the interaction between the researcher and the artist, new inquiries may arise that were not considered in the early stage of the scientific *modus operandi*. One of the objectives is that reconstructing an element of prehistoric life is ultimately plausible and convincing epistemologically. If the paleoartistic work manages to convince in terms of plausibility and scientific consistency, science will then approach society in a more popular and intense way, whether for purely pedagogical, historiographical, or museological purposes. Therefore, paleoart develops a triple facet: aesthetic, historical, and social (Amorós, 2023).

1.3. Need to counterbalance zoocentrism in paleoart

After making the clarification that this is a concept that should not be confused with the art of prehistoric people like rock art, the term "paleoart" was first coined by Hallett (1986), who explains his creative process as work that begins with researching available material, including original fossils, consultations with paleontologists, and studying modern analogue animals. All of this is done before starting sketches of anatomy and scenes for the final painting. For Hallet, paleoart constitutes, in his conceptual expression, an artistic experience strictly related to paleontology, through which the past prehistoric beings' life and behavior in their ecosystems are recreated. It is crucial to emphasise that this zoocentric explanation of the paleoartistic discipline has deep roots (Lescaze and Ford, 2017). Historically, a notable exception is the monumental body of watercolour work developed through close collaboration between the artist Joseph Kuwasseg and the botanist Franz Unger in the mid-19th century (Unger, 1851; Rudwick, 1992). In fact, zoocentrism has also permeated much of evolutionary research, including paleoecology. Beerling (2007) emphasises the neglect of plants in studies of the planet's origin, highlighting the significant role plants have played on Earth: they have sculpted the Earth's composition, participated in geophysical processes such as plate tectonics, produced oxygen, stored carbon, sequestered nitrogen, regulated the atmospheric chemical composition, and, at times, influenced the rate of rock erosion through their roots. Plants also regulate the water cycle and determine how solar radiation is absorbed in the landscape.

In the everyday reality of paleoart, an overwhelming majority of works, whether published or displayed in museums or exhibitions, depict the habitat as context, ornament, or simply the background of the painting to position animals in intentionally more conspicuous perspectives (see Sanisidro and Barrón, 2016; Amorós, 2023 for discussion). The details of anatomy and morphology are, at times, genuine zoological studies, without diminishing the paleoecological information or conflicting with the aesthetic function (https://www.nationalgeographic.es/fotografo/oscar-sanisidro, https://mauricioanton.wordpress.com/). However, plants are occasionally depicted vaguely, leaving the botanist unable to identify the species or group of species. In other instances, the botanical record is well-defined but clearly insufficient. It becomes pertinent to reconsider this zoocentrism in light of the future of paleoartistic research.

2. Objectives and scientific foundation

Even without making a clear distinction between paleoart and scientific illustration (for an in-depth discussion, refer to Amorós, 2023), there is a notable scarcity of pictorial reconstructions specifically centred on Iberian vegetation during the Quaternary (Villaverde, 2001; Amorós et al., 2021; Ochando et al., 2022a, 2022b; Amorós, 2023). However, our paleobotanical understanding of the region has substantially improved in recent decades (for compilations, see: Carrión and Leroy, 2010; Carrión et al., 2022a; 2022b), providing a solid scientific foundation that can serve as a source of inspiration for artistic inspiration. In this paper, we present the results of paleoartistic research aimed at visually reconstructing the vegetation landscapes surrounding the Orce Archaeological Zone (OAZ), which encompasses several sites dating from the period between 1.6 and 1.2 Ma (Agustí et al., 2010; Duval et al., 2012; Toro-Moyano et al., 2013; Lozano-Fernandez et al., 2015) during the Early Pleistocene of the Guadix-Baza Basin in southern Spain (Fig. 1). We wish to emphasise those aspects that may be of greater relevance for understanding paleobotanical findings with a view to their dissemination and teaching. Likewise, this paleoartistic exercise might provide avenues for paleoecological research insofar as there are significant gaps in the inferential power of palynological data, which become much more evident when the aim is to arrange such data visually in a pollen-source area.

The Orce Archaeological Zone (OAZ) is a depression formed after the closure of the Mediterranean-Atlantic gateway during the Messinian (Hüsing et al., 2010; Haberland et al., 2017). Despite being surrounded by forested areas of the Betic Cordillera (Fig. 1), the present-day landscape is characterised by badlands and largely treeless Mediterranean vegetation due to a semi-arid climate and long summer drought. However, during the Early Pleistocene, the region featured wetlands when the large paleo lake Baza was active and cyclically receded, giving rise to freshwater springs, ponds, and pools (Granados et al., 2021; Martínez-Monzón et al., 2022). In this context, the deposition and preservation of the remains of numerous vertebrates, particularly mammals, are located (Maldonado-Garrido et al., 2017). In addition to the paleontological record, there is archaeological evidence of anthropic activities (e.g., Toro-Moyano et al., 2013; Espigares et al., 2019; Titton et al., 2021). Notably, OAZ includes human remains (Toro-Moyano et al., 2013), which, along with the Atapuerca sites (Carbonell et al., 2008; Moreno et al., 2015), are the oldest in western Eurasia for the *Homo* genus, dating back to approximately 1.4 Ma.

The paleolandscape artwork presented here primarily relies on fossil pollen data from three Early Pleistocene archaeological sites within OAZ: Venta Micena 1 (VM1), Barranco León (BL), and Fuente Nueva 3 (FN3) (Ochando et al., 2022b). Preliminary pollen finds in BL and FN3 were reported by Jiménez-Moreno (2003). Additionally, palynological information from the nearby Palominas paleolake (Altolaguirre et al., 2019; 2020) has been taken into account. VM1 (c. 1.6 Ma) is characterised by the dominance of *Ephedra, Pinus, Juniperus, Artemisia*, Poaceae, and evergreen *Quercus*, with smaller contributions from Amaranthaceae, Asteraceae, *Olea*, deciduous *Quercus, Alnus, Castanea, Fraxinus, Salix, Phillyrea,* Genisteae, and *Erica*. Other ecologically significant taxa include *Maytenus* and Cyperaceae. The total arboreal pollen is generally below 40%, indicating a vegetation adapted to sunny conditions. Trees were likely concentrated in habitats with soil moisture, such as river and lake edges, and valleys between mountains. The prevalence and exceptional abundance of *Ephedra distachya-nebrodensis* suggest a Mediterranean steppe landscape, including thermophilous species like *Maytenus senegalensis* and *Olea europaea*. Among the three pollen records studied, VM1 undoubtedly provides the most consistent indicators of local aridity. A total of 32 pollen taxa were identified (Ochando et al., 2022b).

BL (c. 1.4 Ma) is characterised by the dominance of Poaceae, *Juniperus, Olea, Pinus,* evergreen *Quercus, Cistus, Artemisia*, and Cichorioideae. Other ecologically significant taxa include deciduous *Quercus,*

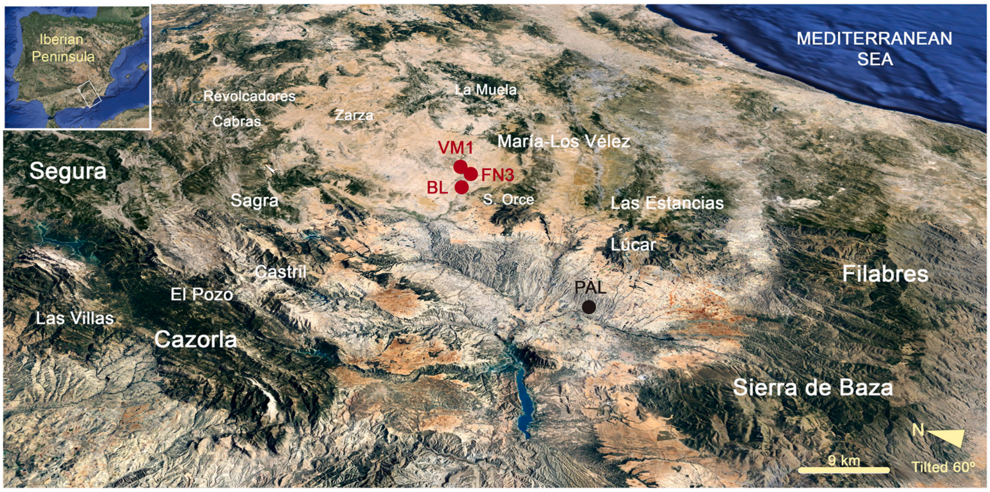

Fig. 1. Geographic location of the Archaeological Zone of Orce (OAZ) in southeastern Iberian Peninsula. The archaeological pollen records forming the basis of the artistic reconstructions in this work are symbolized by BL (Barranco León), FN3 (Fuente Nueva 3), VM1 (Venta Micena 1). Another reference pollen sequence (PAL: Palominas) corresponds to a paleolacustrine area. OAZ is surrounded by mountains (Baza-Filabres, Segura, Cazorla, Las Villas, Las Cabras, Castril, El Pozo, La Sagra, La Zarza, Lúcar-Las Estancias, María-Los Vélez, Orce) and lies on the edge of a large depression that was occupied in the Early Pleistocene by a large lake (Baza paleolake) surrounded by a complex and extensive river network, of which today some rivers remain, as well as gullies and seasonal streams between badlands. Modified from Google Earth (2023).10.49.0.0. https://www.google.es/earth/.

Alnus, Betula, Corylus, Carpinus, Fraxinus, Ulmus, Juglans, Castanea, Populus, Salix, Arecaceae, *Sambucus, Pistacia, Maytenus, Ephedra fragilis*, Lamiaceae, and Cyperaceae. The inferred arboreal cover fluctuates throughout the sequence, ranging from approximately 27%–55%. Noteworthy is the coexistence of xerophytes (*Lygeum, Capparis,* Zygophyllaceae), deciduous trees, and Tertiary relics such as *Carya, Eucommia, Pterocarya*, and *Zelkova*. The co-occurrence of *Pistacia, Maytenus, Olea,* and Arecaceae is particularly worth mentioning, which suggests thermicity. A total of 53 pollen taxa were identified (Ochando et al., 2022b).

FN3 (c. 1.2 Ma) is characterised by the dominance of evergreen *Quercus, Pinus* (including *Pinus pinaster*), *Juniperus, Olea*, and Amaranthaceae, along with lesser contributions from deciduous *Quercus, Castanea, Populus, Salix, Ulmus, Fraxinus, Pistacia, Phillyrea,* Genisteae, Poaceae, Asteraceae, *Erica, Cistus*, and *Ephedra fragilis*. Other ecologically significant taxa include *Quercus suber, Alnus, Carya, Fagus, Juglans, Sambucus ebulus, S. nigra, Maytenus, Sorbus,* Lamiaceae, *Typha*, and Cyperaceae. The presence of Arctotertiary taxa such as *Carya* is worth mentioning. Arboreal pollen exceeds 50% and often surpasses 70% across the sequence. A total of 60 pollen taxa were identified (Ochando et al., 2022b).

Regarding the chronology of the study sites in OAZ, it is important to bear in mind that the previously mentioned dates (1.6, 1.4, 1.2 Ma for VM1, BL, and FN3, respectively) are averaged approximations (see Duval et al., 2012; Toro-Moyano et al., 2011, 2013). Although with palynological hiatuses, the three sequences cover a longer time interval, and there are also uncertainties associated with the methodological challenges in the geochronology of this type of record.

The Palominas lake pollen sequence (c. 1.6–1.1 Ma) (Fig. 1) encompasses ten climate cycles driven by obliquity forcing (Altolaguirre et al., 2019, 2020, 2021). The prevalence of *Artemisia*, Amaranthaceae, Poaceae, Asteraceae, and open woodlands characterises cold, dry periods. Warm, humid periods involve the dominance of Mediterranean formations. Similar to the OAZ sites, Palominas displays the prevalence of evergreen *Quercus, Juniperus*, and *Pinus* among arboreal taxa. Mesophytes include deciduous *Quercus, Alnus, Corylus, Betula, Fraxinus, Ulmus, Salix, Populus, Carpinus, Castanea, Celtis, Juglans*, and *Myrica*, among others. Local wetland vegetation expanded during interstadials and interglacials. This pollen record also includes Tertiary relics such as *Cathaya, Tsuga, Parrotia, Eucommia, Pterocarya,* and *Zelkova*.

It is worth considering that the taphonomy of pollen spectra in a lacustrine sequence differs from that of paleontological or archaeological sites. In the former case, a predominance of wind-pollinated species is expected, some with long-distance transport. Archaeopalynological samples, on the contrary, will exhibit both pollen and spores from both anemophilous and zoophilous plants, with the incidence of local pollen transport usually being higher (Navarro et al., 2000, 2001; Carrión, 2002a; Hunt and Fiacconi, 2018; Carrión et al., 2009). In this regard, some taxa with strict zoogamy may be exclusive to archaeopalynological records, as is the case with *Maytenus, Ziziphus*, and *Calicotome*, absent in Palominas (Ochando et al., 2022b). Both sources of information complement each other, and their concurrences reinforce paleoecological interpretation (Carrión et al., 1999, 2009, Carrión, 2022d).

Altogether, the pollen data define a mosaic vegetation landscape influenced by the geophysical context. Plausibly, this dependence should extend to whether substrates were calcareous (e.g. *Quercus faginea, Pinus nigra*) or siliceous (e.g. *Q. pyrenaica, P. sylvestris*), the altitude, groundwater levels, local rainfall, continentality, or the patchy presence of gypsum deposits. Studies on Early Pleistocene faunas in OAZ reveal the existence of several climatically-driven phases. However, two prominent patterns emerge from all paleoenvironmental inferences based on rodents (Agustí et al., 2009, 2010), herpetofauna (Blain et al., 2016; Sánchez-Bandera et al., 2020), and large mammals (Martínez-Navarro et al., 2003; Espigares et al., 2013; Saarinen et al., 2021). Firstly, there is evidence of relatively temperate conditions prevailing most of the time, often resembling current conditions. Secondly, and more importantly, there is frequent and paleogeographically widespread occurrence of humid biotopes, likely influenced by upwellings, elevated water tables, or directly associated with water bodies, including lacustrine, brackish, and riparian environments. These can be regarded as hydroclimatic refuges, which, in retrospect, would have been more apparent during interglacial and interstadial phases. Paleoartist Mauricio Antón has depicted all this paleofaunistic work with great precision and resonance in various works (Arribas and Palmqvist, 1998; Palmqvist et al., 2007, 2008a, 2008b, 2011; Espigares et al., 2013, 2021; García-Aguilar et al., 2014; Martínez-Navarro and Sala, 2016).

In the pursuit of reconstructing these paleoecosystems, it is crucial to note that, based on our current knowledge, the ecological requirements of the taxa involved have not undergone substantial changes during the studied period (Suc, 1980; Leroy, 1990; Carrión and Leroy, 2010;

Altolaguirre et al., 2020). There are currently no analogous plant communities to the pollen spectra discovered in OAZ, which is not surprising, as floristically defined plant associations exhibit a relatively ephemeral duration in the broader context of the Pleistocene, including within the Holocene (Carrión et al., 2022a, b). However, the combination of species in the Early Pleistocene of OAZ, including Iberian-North African, Holarctic, Mediterranean taxa, and survivors from Tertiary floras, is undoubtedly distinctive (Ochando et al., 2022b). It is associated with a unique combination of species that maintain their distribution area, others that arrive in the territory, and others that will later become extinct regionally, albeit in episodes delayed compared to the rest of the continent (Carrión et al., 2022a, b). In the context of the

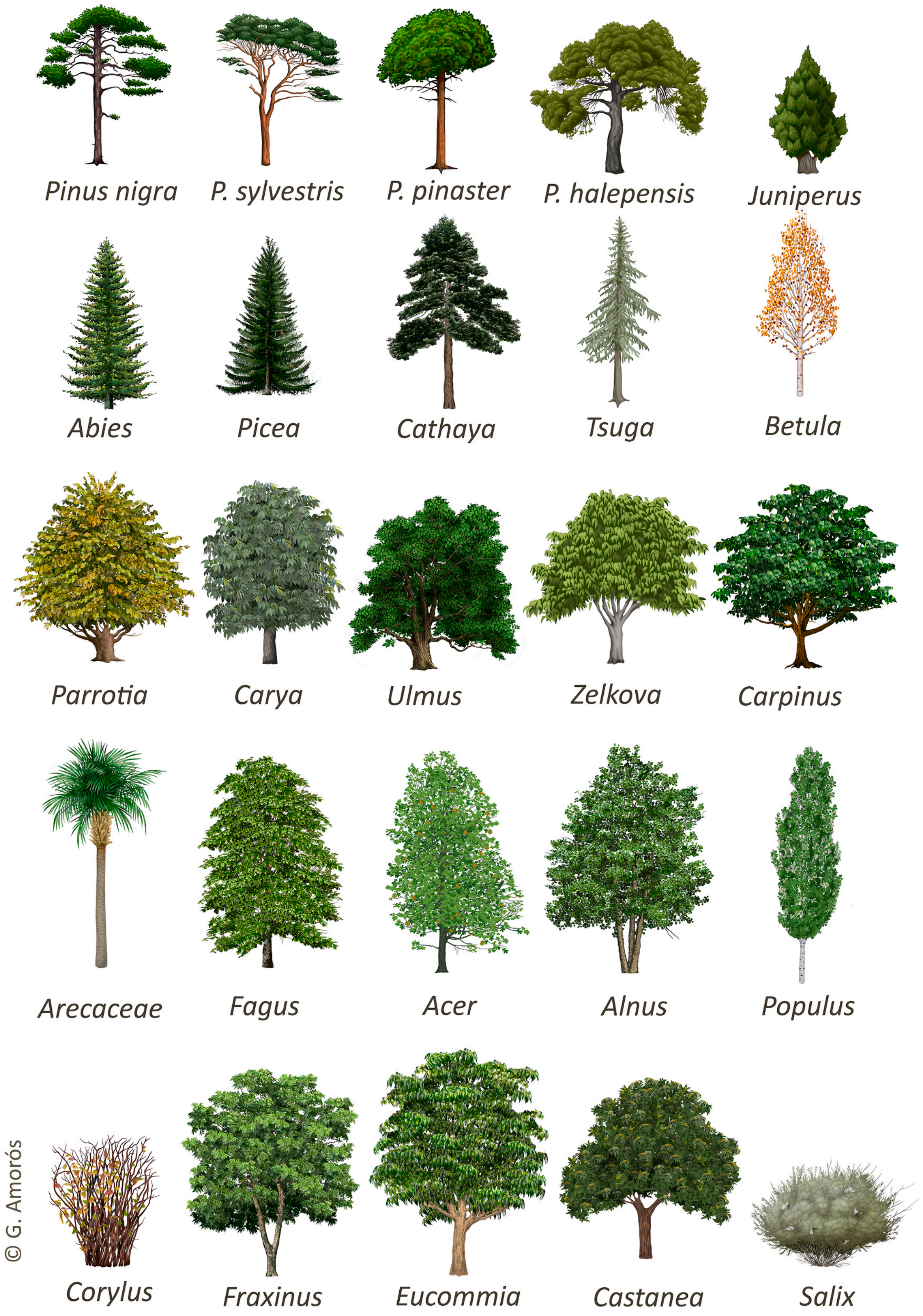

Fig. 2. Original digitised drawings depicting the primary taxa of the paleoartistic reconstruction of the Orce Archaeological Zone (OAZ) shown in Figs. 3–6 (part 1).

European Cenozoic, the Iberian Peninsula attracts attention because major biotic crises occurred at the end of the Oligocene (c. 28-23 Ma), during the Piacenzian (3.6–2.5 Ma), and the Early-Middle Pleistocene transition (1.4–0.7 Ma) (Carrión and Fernández, 2009; Postigo-Mijarra et al., 2009). Still, the coalescence of survivors and immigrants makes the Early Pleistocene a highly distinctive period from a phytogeographical perspective. The survival of Pliocene floras in the Iberian Peninsula (Leroy, 1997; Postigo-Mijarra et al., 2007; Barrón et al., 2010; González-Sampériz et al., 2010; Magri et al., 2017; Verdú et al., 2020) must have been therefore contingent on Early Pleistocene vegetation dynamics (Carrión et al., 2022a, b), although there are latitudinal differences including denser forest formations in the northeast, and arid lands in the south (Suc and Cravatte, 1982; Leroy, 1987, 1988, 1997; Postigo-Mijarra et al., 2007; Jimenez-Moreno et al., 2010; Altolaguirre et al., 2019). Several cases of survival are particularly relevant, such as *Carpinus betulus,* which might have its last refuge in the Betics before retreating to positions that today are confined to the Eurosiberian belt (Ochando et al., 2022b). Their illustration in this study attempts to

Fig. 3. Original digitised drawings depicting the primary taxa of the paleoartistic reconstruction of the Orce Archaeological Zone (OAZ) shown in Figs. 3–6 (part 2).

honour this circumstance in the geographic history of the species. In the case of *Eucommia* and *Zelkova,* the Orce region is probably the last peninsular refuge (Altolaguirre et al., 2020).

3. Drive behind creative decision

For this paleolandscape artwork, we have chosen the Orce region due to its archaeological and paleontological significance. An undeniable attraction was to depict the landscape surrounding the earliest Europeans. Another crucial aspect is the geographic position of OAZ, situated not far from the Mediterranean sea, and at the ecotone between dry depressions and high mountains, with highly complex and rugged orographic systems, where even today, plant diversity is extraordinary (Castroviejo, 2020; Devesa and Martínez-Sagarra, 2023). Notably, the Betic mountain ranges significantly contribute to the Mediterranean hotspot (Molina-Venegas et al., 2017). In addition, the Pleistocene climatic records of the region suggest climatic fluctuations that leave their mark on floristic assemblages and vegetation types, although without the taxonomic amputation seen in higher latitudes (Magri et al., 2017; Carrión et al., 2022a, b). This role as a peninsular refuge is intrinsic to the Iberian Quaternary but reaches its climax at the onset of the Pleistocene. Climatic variability, coupled with plant resilience and floristic survival phenomena, creates a fertile and inspiring stage for paleoartistic illustration.

4. Paleoartistic works

4.1. General and methodological considerations

After painting the taxonomic elements selected (Figs. 2 and 3) using the methods in Amorós (2023), four paleolandscape digital paintings were created (Figs. 4–7). Obviously, numerous artistic styles can potentially illustrate a plant community in space. Our choice has been to reduce some realism to gain taxonomic prominence while simultaneously addressing the geobotanical landscape synoptically. A drawing attempting photorealism could generate an image too homogenous in shapes and colours to discriminate between plant species, genera, and families. To the extent possible, we have tried to include identifying features that provide contrast, such as fruits (*Sorbus, Arbutus, Salix, Castanea, Myrtus, Pistacia*, Cyperaceae), flowers and inflorescences (Asteraceae, *Artemisia*, Lamiaceae type *Lavandula*, Cistaceae, Genisteae, *Typha, Erica, Sambucus-Viburnum*), sparse groups of deciduous leaves (*Betula, Juglans, Acer, Parrotia, Corylus, Populus*), or even growth habits with certain “cultural” concessions (e.g., anthropic forests), which likely do not correspond to the wild morphotypes but facilitate visual discrimination. We are aware that this style may also produce phenological distortions (e.g., overlapping marcescent phases in some species with foliage phases in others). With the same goal, the drawings tend to isolate each plant individual of each taxon without substantially

Fig. 4. Paleoartistic reconstruction that, regardless of the climatic phase, summarises the main taxa and vegetation types of the Early Pleistocene (1.6–1.2 Ma) inferred from palynological findings in VM1, BL, and FN3, Orce Archaeological Zone (OAZ). It includes altitudinal gradients culminating in conifers and birches above deciduous forest belts, areas with deeper soils in valleys dominated by woody angiosperms, and finally lacustrine and riparian environments at the bottom with meadows, sedge communities, and phreatophytes. The rhinoceros (bottom right) symbolises the importance of herbivory in the heliophytism of Pleistocene forests in the region.

Fig. 5. Paleoartistic reconstruction of a riparian environment under arid conditions during a stadial phase of the Early Pleistocene in OAZ, such as inferred from the paleoecological record of VM1 around 1.6 Ma. A greater proliferation of trees is observed in areas influenced by the water table. There are also pines and oaks alongside the arboreal strata that make up the gallery forest. The locally abundant *Ephedra* is depicted in rocky areas and substrates with marl and gypsum. Halophytic communities are largely in the lower part of the drawing. *Artemisia* abounds in the rocky, treeless slopes.

modifying the outline. Again, this creates an implicit tension between style, physiognomy, and ecology, but in the study case, paleoart should not operate at the expense of scientific transmission. This choice also explains some decisions in colouration. For example, although obviously, not all chenopods exhibit betacyanins in their vegetative organs, nor throughout their life cycle, we have decided to colour them red as it is a very distinctive feature of the family that highlights its presence among the more xerophytic and halophytic communities of the region (Figs. 4 and 5).

The palynoanalytical capacity to separate plant taxa is another critical factor influencing the reconstruction, given the lack of macrofossils or aDNA studies that would allow taxonomic refinement. This forces us to make pictorial decisions that underrate paleobiological diversity. For example, we have opted for a morphotype *Juniperus thurifera-phoenicea* for Cupressaceae, overlooking the more probable occurrence of other species with needle-like leaves of the *J. communis-oxycedrus* type. When possible, species have been distinguished, such as the grass *Lygeum spartum*, indicative of arid and marly soils.

4.2. Vegetation landscape mosaic

Fig. 4 shows a schematical outline of the OAZ paleoecological inferences without distinguishing between climatic phases. The regional landscape mosaic is illustrated here with particular attention to altitudinal zones (upper part featuring high mountain conifers and birches, middle part with Mediterranean conifers and some deciduous species, and the lower part representing most woody angiosperms on deeper soils), shrub communities on lithosols in summit areas and steep slopes, and communities of hygro-hydrophytes (including trees) associated with water bodies (bottom part). The presence of a rhinoceros (*Stephanorhinus etruscus*) in the lower right corner and the openness (heliofitism) of the forests aim to indicate the impact of large mammalian herbivory on vegetation structure. The recent work of Pearce (2023) and Pearce et al. (2023), although related to higher latitudes in a more recent period (Last Interglacial period at 129,000–116,000 years ago), confirms this assumption: the European temperate forest biome did not have a closed canopy but, due to the disturbance of large herbivores, remained heterogeneous rather than uniformly dense. Forest coverage might be certainly greater in warmer phases and lower in colder and drier ones. However, tree elements do not disappear in the latter, nor are there substantial floristic variations within a relatively heliophytic forest framework.

4.3. Riparian vegetation in arid context: hydroclimatic refugium

Fig. 5 emphasises the results of VM1, illustrating what could have been a semi-arid landscape where a more significant proliferation of trees could be expected in areas influenced by the water table. In this case, we have selected a riparian stretch surrounded by slopes with open vegetation. As commented above, it is clear that ravines and watercourses were widespread, with episodic stream flows occurring. Undoubtedly, these would be disruptive to the marginal vegetation of the hydrographic network, which would be adaptively equipped for recovery. Over time, these phenomena would intensify, leading to the ravining that characterises the present denuded landscape. It is worth noting that we have included some pines and oak species alongside the arboreal strata that make up the gallery forest. This combination seems plausible to us, with water being the limiting factor. It is a phenomenon observed today in riparian zones, seasonal watercourses, and ravines in the semi-arid Iberian Mediterranean (Blanca et al., 2011). Also, with an

Fig. 6. Paleoartistic reconstruction of a glacial refuge for mesothermophilous plants located in an intramontane valley within the Betic Cordilleras surrounding the Guadix-Baza depression. This scenario embraces the period 1.6–1.2 Ma. Here we emphasise the coalescence in space and time of taxa with different ecological affinities in a climatic context where survival in hydroclimatic refuges would be the limiting chorological factor. Refuges may have been located at mid-altitudes, within what are now the supra and mesomediterranean vegetation belts. Pine forests dominate on rocky soils on steeper slopes, and angiosperms' greater density and arboreal diversity are seen within valley bottoms. The occurrence of genera such as *Cathaya, Picea, Abies, Tsuga, Parrotia, Carya, Zelkova, Carpinus, Eucommia, Arbutus, Sorbus, Fagus, Acer, Juglans, Castanea*, and *Ulmus*, among others, is worth mentioning.

actuo-ecological approach, we place the locally abundant *Ephedra distachya* in rocky areas and substrates with marl and gypsum (López-González, 1986).

Halophytic communities are primarily depicted in Fig. 5. Plausibly, their floristic composition would not be very different from the present, featuring species from the Amaranthaceae family like *Suaeda vera, Arthrocnemum macrostachyum, Salsola oppositifolia, Sarcocornia fruticosa*, Asteraceae such as *Inula crithmoides*, and a variety of species of *Plantago, Juncus, Frankenia*, and *Limonium* (Valle et al., 2004; Blanca et al., 2009). Other communities with edaphic stress, in drier slope soils, could also contain Amaranthaceae (Fig. 3) but would be occupied mainly by grasses like *Stipa tenacissima, Lygeum spartum, Dactylis glomerata, Brachypodium retusum*, Asteraceae (*Carduus, Helichrysum, Launaea, Centaurea, Santolina*), Lamiaceae (*Sideritis, Thymus, Lavandula, Rosmarinus*), Cistaceae (e.g. *Cistus clusii*), and Fabaceae (e.g. *Ulex, Genista*).

4.4. Mountain refugium

In Fig. 6, we conceptualise a glacial refugium for woody plant diversity located in an intramontane valley within the Betic Cordilleras surrounding the Guadix-Baza depression. This could correspond to a valley in the current Sierras de María-Los Vélez (2045 m asl), Baza-Filabres (2269 m asl), Castril (2106 m asl), El Pozo (2027 m asl), La Sagra (2383 m asl), Orce-La Umbría (1826 m asl), La Zarza (1499 m asl), Lúcar and Las Estancias (1720 m asl), Cazorla (1848 m asl), Segura (1993 m asl), Las Villas (1831 m asl), or Las Cabras (m asl) and Revolcadores (m asl) further east (Fig. 1). We emphasise the coalescence in space and time of taxa with different ecological affinities in a climatic context where survival in hydroclimatic refugia would be the limiting chorological factor. We metaphorically refer to it as Noah's Ark for mesothermophilic species. This image is based on data from OAZ but also finds reinforcement in previous palynological studies in the Betic mountain region, especially during the Late Pleistocene (Carrión, 2002b; González-Sampériz et al., 2010; Manzano et al., 2017; Verdú et al., 2020; Camuera et al., 2022; Carrión et al., 2022b). These refugia may have been located at mid-altitudes, within what is now the supra and mesomediterranean vegetation zones, which must have been closer and interconnected (Carrión, 2002a). We found it interesting to highlight the occurrence of pine forests on rocky soils on steeper slopes and the greater density and arboreal diversity in valley bottoms on deeper, moist, and organic soils. This is the work in which we have made the most significant effort to emphasise the occurrence of genera such as *Cathaya, Picea, Abies, Tsuga, Parrotia, Carya, Zelkova, Carpinus, Eucommia, Arbutus, Sorbus, Fagus, Acer, Juglans, Castanea*, and *Ulmus*, among others. In the lower right, we highlight a mixed *Quercus* forest.

4.5. *Homo* forest habitat

In Fig. 7, we provide a detailed view of Fig. 6, incorporating an individual of *Homo* and another of *Natrix* (grass snake) on a branch of the Tertiary relic *Eucommia*. The snake, a semi-aquatic colubrid, is found in the paleontological record of OAZ, and we have depicted it in recognition of the fruitful herpetological work conducted (Blain et al., 2011, 2016; Sánchez-Bandera et al., 2020, 2023) and the paleoecological indication of the existence of freshwater environments. The human fossil remains correspond to a milk tooth from a child of approximately 10

Fig. 7. About 1.4 million years ago, a female *Homo* (here named the "Lozana Andaluza") and an individual of *Natrix* (grass snake) on a branch of the Tertiary relic *Eucommia* within a glacial refuge (Fig. 5). The artistic ensemble aims to place these early *Homo* individuals in their vegetation landscape. The combination of *Homo* and *Natrix* in a pristine environment is reminiscent of the *Book of Genesis* (Eve tempted by the apple).

years old (Toro-Moyano et al., 2013). The artistic ensemble aims to place these early *Homo* individuals in their habitat of vegetation and flora. There are no further bone records to identify the hominin species or the sex of the individual found. Nor do the archaeological data allow us to infer the biological species responsible for the lithic industry. Therefore, we have taken the conjectural liberty to go against what we understand are cultural prejudices in much of the iconographic literature on extinct hominins taxa or even paleodemes (see Zollikofer and Ponce de León, 2010; Amorós, 2023; Finlayson et al., 2023 for discussions). Thus, for our protagonist, we opted for (i) female sex, (ii) smooth and dark skin, (iii) long, black, curly, and abundant hair, (iv) relatively derived or "human-like" morphological features. It is worth noting that variability within a taxon (e.g., species) or even within a paleodeme may be due to different factors (age, sex, pathology, activity, etc.). An example of high phenotypic diversity in a population restricted in time and space is found in the Early Pleistocene site of Dmanisi (Georgia: 1.8 Ma) (Ferring et al., 2011). There, four of the five skulls unearthed correspond to individuals with very different ontogenetic stages, genders, dental wear stages and dentoalveolar remodeling (Lordkipanidze et al., 2013; Margvelashvili et al., 2013; Zollikofer et al., 2014). One of the gracile crania is D2282, which has been characterised as a young female (Rightmire et al., 2017).

As discussed by Amorós (2023), although with notable recent exceptions, paleoart focused on the face and body of hominins before the appearance of anatomically modern humans has traditionally had a primitivist, even ape-like bias (e.g., exaggerated prognathism, very long arms, abundance of body hair, expression of cognitive deficit). We know that long hair would have provided an adaptive advantage in this climatic context. Lasisi et al. (2023) present empirical evidence showing that tightly curled hair would have offered increased protection against heat gain from solar radiation. In addition, similarly to a previous work depicting Middle Pleistocene Neanderthals (Ochando et al., 2019; Amorós et al., 2021), we have endeavoured to avoid conventional scenes of hunting, fishing, cannibalism, or meat consumption routines, as the region was rich in edible plants (Altolaguirre et al., 2021; Ochando et al., 2022b). In addition, the importance of primary producers in sustaining animal life in a territory is also emphasised. Thus, as highlighted by Saarinen et al. (2021) there were productivity thresholds in the Guadix-Baza Basin below which human presence was improbable.

We have adopted a relaxed attitude for the woman to emphasise the inhabitants' knowledge of the habitat in this region. In a way, we aim to convey that the woman "knows" that *Natrix* is not a venomous species.

She is unarmed and not in a defensive posture. Our intention, following the German biophysical tradition (von Uexküll, 1928), is to shed some light on the *Umwelt* of *Homo*, that subjective and space-temporal reality in which every living being interacts. Following this approach, the woman has been named "Lozana Andaluza" (Andalusian Wily Woman). "La Lozana Andaluza" is the title of an emblematic novel for Andalusia, written by the Spanish cleric Francisco Delicado and published in Venice in 1528 (Delicado, 2013). The novel portrays a beautiful and clever woman who perfectly understands a challenging social context and survives by showing an extraordinary capacity for adaptation (Cáseda, 2019). The work has significantly impacted Spanish culture, and, in fact, the term "lozano/a" is often used to refer to healthy individuals. Interestingly, it is also used to describe intensely green, lush, and leafy plants.

5. Concluding remarks

Based on palynological data, we pictorially represent a glacial refuge of plant species in the southern interior of the Iberian Peninsula during the Early Pleistocene. This includes attention to the possible distribution of altitudinal zones, the taxonomic and physiognomic diversity of vegetation, including taxa whose current geographical position is very distant from the study area, taxa that became extinct in the Iberian Peninsula in phases later than the Early Pleistocene, or taxa that had previously gone extinct at higher latitudes in the European continent. This paleolandscape art also aims to visualise the coexistence of mesophytic, thermophytic, and xerophytic plant communities during the Early Pleistocene. The Iberian Peninsula is a complex territory with an unstable hydrographic network, which has also experienced convulsive Neogene tectonics, with phases of insularity promoting geographical isolation and allopatric speciation. It is a region that involves late Cenozoic contacts between Europe, North Africa, and Western Asia, promoting migrations and disjunctions (Barrón et al., 2010; Postigo-Mijarra et al., 2010; Carrión et al., 2022a). These geohistorical contingencies explain much of the high floristic diversity of the southeastern. Our contribution also aims to reflect one of the last phases of glory of the great Tertiary forests in Europe.

In connection with the former, here we try to recall that the archaeological study area includes some of the oldest evidence of European hominins, around 1.4 million years ago. The illustration in Fig. 7 reflects the research experience and perspective of the authors regarding the habitat of the earliest *Homo* in the Iberian Peninsula. It is worth recalling the work of Carrión et al. (2011), which visualises how the regions where the first fossils of each hominin taxon were found coincide with the distribution of biodiversity hotspots in Africa, Asia, and Europe. Biodiversity hotspots are physiographically and biotically complex territories with high taxonomic and ecological disparity that have efficiently absorbed environmental impacts over deep time. These territories have served as engineers of terrestrial species, including hominins and as reservoirs of biodiversity during episodes of geophysical and climatic disruption (Carrión et al., 2019). The primary hotspot for human evolution is undoubtedly the Horn of Africa (Barboni et al., 2019). However, the Mediterranean Basin contains regions with high speciation activity (Bennett et al., 1991), and the Betic Cordilleras and the southernmost tip of the Iberian Peninsula are also spaces for innovation where human evolution should not be excluded.

Visualising these early *Homo* surrounded by Tertiary relics in open sylvatic ecosystems rich in resources pays homage to pertinent research performed in the Iberian Peninsula (e.g. Finlayson, 2004; Finlayson and Carrión, 2007; Leroy et al., 2011; Magri et al., 2017; González-Sampériz et al., 2020; Carrión, 2022a; 2022b, 2022c, 2022d) where even later, during the Middle and Late Pleistocene, *Homo heidelbergensis* and *H. neanderthalensis* show preference to arboreal and high scrub ecosystems (Carrión and Walker, 2019; Carrión et al., 2003, 2008, 2018, 2019; Finlayson, 2009; Stewart et al., 2019; Ochando et al., 2020a, 2020b, 2022a). Using a different proxy, the avian fauna for Pleistocene sites of the Palearctic, Finlayson et al. (2011) showed a striking association between *Homo* and habitat mosaics. In particular, a mix of open savannah-type woodland, wetlands and rocky habitats, a trend observed from the earliest populations of the Early Paleolithic to the latest hunter-gatherer communities of the Upper Paleolithic. In perspective, it could be argued that the niche of *Homo* has become any conceivable niche.

There is, finally, a playful element in the Figura 7 artwork that will not escape the reader: the combination of a *Homo* female and *Natrix* in a pristine environment is reminiscent of a cardinal episode from the *Book of Genesis* (Eve tempted by the apple) in Judeo-Christian mythology, ultimately a cultural element of Eurasian origin. The composition is also a wink to the significance of early paleoart steps (17th-18th centuries). These illustrations, aligning with the sequential biblical narrative of the antediluvian period, depicted untamed landscapes "before the existence of (wo)man" (Amorós, 2023). The most extensive work of this paleo-Christian visual expedition was Johann Jakob Scheuchzer's "Physica Sacra," published between 1731 and 1735. While much scientific progress has transpired since those early days, the field of paleoart has weathered numerous challenges, sidelining the botanical aspect that once enjoyed the prominence seen in those groundbreaking pioneer works (Unger, 1851; Ludwig, 1861; Rudwick, 1992; Amorós, 2023). In this contribution, we aim to forge new paths in the representation of paleovegetation landscapes, recognising the pressing need for taxonomic exploration. We cannot demand any less detail than what is granted to animals, but rather the same paleontological devotion. In any case, we acknowledge our pursuit of the aesthetic surprise inherent to every paleoartistic endeavour: the thrill of envisioning a lost world originally and distinctively. We fully comprehend that this work will be judged not only by its scientific accuracy but also by the magnitude of the emotional response it can evoke.

CRediT authorship contribution statement

José Carrión: Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Gabriela Amorós:** Writing – original draft, Visualization, Software, Methodology, Investigation, Data curation, Conceptualization. **María Victoria Sánchez-Giner:** Supervision, Methodology, Investigation. **Ariadna Amorós:** Writing – original draft, Methodology. **Juan Ochando:** Writing – review & editing, Formal analysis, Data curation, Conceptualization. **Manuel Munuera:** Writing – review & editing, Supervision, Methodology. **Ana Belen Marín-Arroyo:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Juan Manuel Jiménez-Arenas:** Writing – review & editing, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

This research has been primarily funded by the projects HOMEDSCAPE, PID 2022-136832NB-100, Ministerio de Ciencia e Innovación, Spain; SUBSILIENCE Call H2020-ERC-2018. CoG N. 818299, SUMHAL: Conservation of plant diversity in the Betic ranges, LifeWatch FEDER, and LWE 2021-03-033. We have also been supported by the Consejería de Turismo, Cultura y Deporte (Junta de Andalucía, Spain) through the General Research Project (2023–2026) "Evolución humana y paleoecología a partir de los yacimientos pleistocenos de la Zona

Arqueológica 'Cuenca de Orce'. Retos y desafíos" (Ref: SIDPH/DI/MCM). In addition, we are grateful to project PID 2021.125098NB.I00 funding by MICIU/AEI/10.13039/501100011033 and by FEDER, UE, and ProyExcel_00274 funding by Dirección General de Planificación de la Investigación (Consejería de Universidad, Investigación e Innovación, Junta de Andalucía).

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